

A TAXONOMIC REVISION OF *PODOCARPUS*
VIII. THE AFRICAN SPECIES OF SECTION *EUPODOCARPUS*,
SUBSECTIONS A AND E

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THE SECTION *Eupodocarpus* of the genus *Podocarpus* is well represented on African mountain slopes from the southernmost coast to well north of the equator in both the eastern and western regions, wherever relatively cool and wet climates are found. In many regions the species are found in pure stands, often of magnificent timber which has been very important economically. In other parts the members are less abundant, interspersed among other trees, but still constituting an item in the lumber industry. The five species on the continent (all in subsection A) are *Podocarpus elongatus* (Ait.) L'Hérit., *P. Henkelii* Stapf, *P. latifolius* (Thunb.) R. Br. and *P. milanjanus* Rendle, which have been compared by Stapf (10) and Chalk et al. (3), and *P. ulugurensis* Pilger, which was subsequently described (7). *Podocarpus madagascariensis* Baker, endemic on the island of Madagascar, is also in subsection A and has been treated separately by Laurent (4). *Podocarpus rostratus* Laurent, also confined to the island of Madagascar, is in the new subsection E. Our studies show that *P. rostratus* has close affinities with section *Eupodocarpus*, but we recommend placing it in a separate monospecific subsection. Details leading to this decision are to be found under the discussion of the species.

The leaf anatomy of the group consisting of *P. elongatus*, *P. latifolius*, *P. Henkelii*, *P. milanjanus* and *P. madagascariensis* is quite similar, displaying only very minor variations. It always shows two marginal resin canals, hypoderm between the stomatal rows on the lower side, the Florin ring in the stomatal subsidiary cells, and toothed or pitted walls in the epidermal cells.

In addition, we find that *P. elongatus* can usually be distinguished from the others of the group by the thicker palisade parenchyma of more than one layer and no auxiliary sclereids in the mesophyll. In most specimens there is only one vascular resin canal. In most leaves the upper hypoderm is occasionally interrupted and it has been found that these interruptions

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are accompanied by one to six short rows of stomata in the upper epidermis. Thus, *P. elongatus* is differentially amphistomatic, a unique character in the section *Eupodocarpus*. Vascular sclereids or fibers in *P. elongatus* are rare, and the stomatal rows seem closer together than in *P. latifolius* and *P. Henkelii*. Hypodermal fibers average 12–18 μ in diameter, somewhat smaller than those in the other species.

In some specimens of *P. latifolius* and *P. Henkelii* the leaf characters seem to overlap those of *P. elongatus*, but there are generally three vascular resin canals, continuous upper hypoderm, larger hypodermal fibers (15–23 μ average diameter), stomatal rows somewhat farther apart, palisade parenchyma only one cell-layer thick, auxiliary sclereids in the mesophyll, and no stomata on the upper side.

Podocarpus milanjanus, usually having the margins of the leaves revolute, often has the upper hypoderm interrupted at the point of the turn. There is often much increased sclerification, this appearing in auxiliary sclereids in the mesophyll, heavier walls in the accessory transfusion tissue and more abundant upper and lower vascular fibers. *Podocarpus madagascariensis*, however, shows the most extreme sclerification, affecting most of the mesophyll.

The specimen of *P. ulugurensis* which we examined shows the striking difference of five instead of three vascular resin canals. The two extra ones appear in or very close to the transfusion tissue. Externally, this is the only species with a definitely sulcate upper midvein.

KEY TO SECT. EUPODOCARPUS (AFRICAN SPECIES), SUBSECTIONS A AND E

- Leaves very small; many marginal resin canals, accessory transfusion tissue absent Subsection E. *P. rostratus*.
- Leaves larger; 2 marginal resin canals, accessory transfusion tissue present.
 - Leaves with 5 vascular resin canals; upper midrib sulcate. . . *P. ulugurensis*.
 - Leaves with 1–3 vascular resin canals; upper midrib never sulcate.
 - Leaves narrowly lanceolate, 3.5–6.5 cm. long, 3.5–4 mm. wide, acute to obtuse at tip. *P. elongatus*.
 - Leaves elongate and broader.
 - Adult leaves very large, 7–18 cm. long.
 - Male cone very short, 13 mm. long.
 - Leaves 8–18 cm. long, 8–18 mm. wide; seed 20 mm. long. *P. madagascariensis*.
 - Leaves smaller, 5–7 cm. long, 6 mm. wide; seed 28 mm. long. *P. madagascariensis* var. *rotundus*.
 - Male cone longer, 20–45 mm. *P. Henkelii*.
 - Adult leaves smaller, juvenile often as large as above.
 - Leaves gradually attenuate. *P. milanjanus*.
 - Leaves short rotundate, angustate at tip.
 - Leaves 5–11 mm. wide. *P. latifolius*.
 - Leaves 12–17 mm. wide. *P. latifolius* var. *latior*.

Podocarpus elongatus (Ait.) L'Hérit. in Pers. Syn. 2: 580. 1807; L. C. & A. Richard, Comm. Bot. Conif. 13. 1826; Endlicher, Syn. Conif. 218. 1847; Carrière, Traité Conif. ed. 2, 671. 1867; in part; Parlato

in DC. Prodr. 16 (2): 511. 1868; Van Tieghem in Bull. Soc. Bot. France 38: 169. 1891; Pilger in Pflanzenreich IV. 5 (Heft 18): 89. 1903, in Nat. Pflanzenfam. ed. 2, 13: 247. 1926; Dallimore & Jackson, Handb. Conif. 44. 1923, 1931, 66. 1948; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 279. 1931; Chalk, Burt-Davy & Desch, For. Trees & Timbers Brit. Emp. 1: 24. 1932; Stapf in Fl. Cap. 5 (Sect. 2, suppl.): 8. 1933.

Podocarpus Thunbergii var. *angustifolia* Sim fide Dallimore & Jackson, Handb. Conif. 44. 1923, 1931.

Taxus elongata Aiton, Hort. Kew. 3: 415. 1789; Thunberg, Prodr. Fl. Cap. 117. 1800.

Taxus capensis Lamarck in Encycl. 3: 229. 1789.

Podocarpus elongatus is found on the Cape of Good Hope on Table Mountain above the city of Capetown, and hence was one of the plants early brought from that region. Pilger (6) distinguished it from *P. latifolius* and *P. milanjanus* by its narrow lanceolate-linear leaves. Stapf (10) separated it from *P. Henkelii* by its short straight leaves and fleshy receptacle and from *P. latifolius* by leaves only up to 4 mm. wide. Chalk (3), on the other hand, distinguished it from *P. Henkelii* and *P. latifolius* by its red receptacle (which seems to be in error) and from *P. milanjanus* by leaves shorter and much narrower (2.5–5 cm. \times 2–3 mm.). Of the species studied by Laurent (4), *P. elongatus* has the shortest, narrowest leaves, shorter male cones than those of *P. latifolius* and *P. milanjanus*, the shortest peduncle on the female cone, and the smallest seed. According to the descriptions, the twigs of *P. elongatus* are drooping while those of *P. latifolius* are erect with leaves stiff. We would distinguish it from *P. latifolius* by the consistent absence of auxiliary sclereids, the one vascular resin canal (rarely 3), the interrupted upper hypoderm, and the 1–6 upper rows of stomata. The thick leaves show no tendency to be revolute.

The differences from *P. latifolius* seem to be chiefly relative. Many of the sterile specimens referred to *P. elongatus* which show wider leaves and no stomata in the upper epidermis belong probably to *P. latifolius*, which has considerable range in leaf size and also a much wider geographical distribution. Both these species may be found in the same area, often being collected by an explorer on the same day. Their close similarity and the existence of a number of specimens intermediate between the two definitely suggest hybridization. *Podocarpus elongatus* seems to be chiefly a plant of western Cape Province.

MacOwan 1958, in both the Gray and Kew Herbaria, has two elements on it, the portion with larger leaves being *P. latifolius* and that with small leaves being *P. elongatus*. This latter has both a single vascular resin canal and a few stomata on the upper surface.

In all cases it must be borne in mind that for more than fifty years *P. elongatus* (Ait.) L'Hérit. and *P. falcatus* R. Br. (in section *Afrocarpus*) were almost hopelessly confused in the literature, and the identity of the

actual material discussed must be checked with greatest care. *Podocarpus elongatus* is the only species in the section *Eupodocarpus* with scattered stomata occurring on the upper side of the leaf. This may have been noted by some earlier workers, giving credence to the incorrect determination *P. falcatus*, a species with leaves always equally amphistomatic.

Since *Podocarpus elongatus* (Ait.) L'Hérit. was used by Persoon as the type species for the genus, a most diligent search was made for the type specimen. An original Thunberg specimen of this species is in the Botanical Museum at Uppsala with other plants he collected in and near Capetown in 1773–1774. It is a male specimen with almost mature pollen cones. A female specimen, with immature ovules, was found in the Paris Museum, collected by Sonnerat (Herb. Jussieu 17135) in 1774 in the company of Thunberg on the occasion of his visit to Capetown and ascent of Table Mountain, the site of the former collection. This specimen was probably collected at a later season than the Thunberg specimen. Confusion arose when it was found that a specimen in the British Museum, indicated as the probable type for Aiton's *Taxus elongatus* in his *Hortus Kewensis*, was really *P. macrophyllus* var. *Maki* from Japan. This mistaken identity is reasonable as the male specimens of the two entities are very similar to the naked eye although the leaves of *P. elongatus* are usually narrower. In this case, the leaf anatomy carries the proof of identity. No doubt there are other good specimens in the British Museum that we have not seen, as Stapf (10) mentions one by Masson who accompanied Thunberg in his original travels. Nor have we seen the specimen used by L. C. Richard for his drawing of *P. elongatus* with seeds, in the publication of 1826 (9).

We feel that the designation of the *Thunberg* (male) specimen at Uppsala Botanical Museum and the *Sonnerat* (female) specimen at the Paris Museum as lectotypes will make this species better understood by later investigators. In genera composed of dioecious species it is desirable to designate both male and female specimens. It is to be hoped that the misidentified specimen will be removed from a type-folder.

DISTRIBUTION: South Africa, in forested areas in southwestern Cape Province primarily.

SPECIMENS EXAMINED:

SOUTH AFRICA: Cape Province: Clanwilliam Division: Grarsangen Mt., *Pillans* 8676 (K); * Oliphant's River, Kradouw Krantz, *Pillans*

* The following symbols indicate the herbaria having the specimens cited: Academy of Natural Sciences of Philadelphia (Ph), Arnold Arboretum (A), British Museum (BM), Brussels Botanical Garden (BR), University of California at Berkeley (UC) and at Los Angeles (LA), California Academy of Science (CAS), Chicago Natural History Museum (Field Museum) (F), Cornell University (CU), Gray Herbarium (GH), University of Illinois Herbarium (Ill), Royal Botanic Gardens, Kew (K), Missouri Botanical Garden (Mo), New York Botanical Garden (NY), Rutgers University Herbarium (NJU), Stanford University Dudley Herbarium (DS), United States National Herbarium (US), Uppsala Botanical Museum (UPS), Yale University Herbarium (YU).

5297 (K), *Pearson* 5328 (†K), *Wilson* in 1922 (A—4 sheets); Krakadow Pass, Cedarburg Mts., *Wilson* in 1922 (†A); Ceres, *Munchen* 11764 (†NY), *Pearson* 15551 (†LA). Malmesbury: Paarl Berg, *Prior* in 1946 (K), *Drege* 1839 (K); Stellenbosch, *Miller s.n.* (K), *Garside* 1044 (†K); Robertson, Banks of Breede River, *For. Dept. Pretoria Herb.* 1247 (K), *Wilson* in 1923 (†A—5 sheets). Swellendam Division: Breede River, *Burchell* 7480 (K), *Schlechter* 5652 (K); Table Mtn. *Thunberg s.n.* (†UPS), *Sonnerat* ex Herb. Jussieu 17135 (†P). Albany Division: w. of Grahamstown, *Zeyher* 3448 (K), *MacOwan* 1958, in part (†GH, †K); Olijantshoek, *Zeyher s.n.* (†A); Steudel, Eptingee, *Ecklon* in 1834 (†NY); Bain's Kloof, *Hutchinson* 1008 (†K); Kaffraria, Dohne, *Sim* 19620 (†A). LOCALITY NOT INDICATED: ex Hook. Herb., *Pappe s.n.* (K), *Anon.* in 1906 (A), "Hort. Daudin" in 1851 (†DS), *Prager s.n.* (†CAS), *Ecklon & Zeyher s.n.* (†Mo), *Marloth* 11488 (†A), "EM" 81 (†Mo).

CULTIVATED: Algeria For. Sta., *Wilson* in 1922 (A), Piquetberg, Bosch Kloof, *Compton* 9498 (†Ill). U.S., Mass., Arnold Arboretum 482.29, *Judd* in 1930 (A).

Podocarpus latifolius (Thunb.) R. Br. ex Mirb. in Mém. Mus. Nat. Hist. Paris 13: 75. 1825; Berthold, Vergleichenden Anatomie der Coniferen-Blättern 12, 16. 1875; Zimmerman in Flora 63: 2. 1880; Pilger in Pflanzenreich IV. 5 (Heft 18): 90. 1903; in Nat. Pflanzenfam., ed. 2, 13: 247. 1926; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 279. 1931; Stapf in Fl. Cap. 5 (Sect. 2, suppl.): 5. 1933; Dallimore & Jackson, Handb. Conif. 48. 1923, 1931, 72. 1948; Chalk, Burt-Davy & Desch, For. Trees & Timbers Brit. Emp. 1: 23. 1932; Chalk et al., For. Trees & Timbers Brit. Emp. 3: 81. 1935; Adamson in Fl. Cap. Penin. 31. 1950.

Podocarpus Thunbergii Hook. in London Jour. Bot. 1: 657. 1842; Endlicher, Syn. Conif. 217. 1847; Carrière, Traité Conif. ed. 2, 710. 1867; Mahlert in Bot. Centralbl. 24: 281. 1885; Parlatore in DC. Prodr. 16 (2): 511. 1868.

Podocarpus Thunbergii var. *latifolia* Sim fide Dallimore & Jackson, Handb. Conif. 48. 1923, 1931; Van Tieghem in Bull. Soc. Bot. France 38: 169. 1891.

Podocarpus Sweetii C. Presl in Bot. Bemerk. 110. 1844.

Nageia latifolia O. Kuntze in Rev. Gen. 2: 800. 1891 (not Gordon).

Taxus latifolia Thunb. Prodr. Fl. Cap. 117. 1794–1800 et Fl. Cap. (ed. Schultes) 547. 1823.

This species is very large, often found very abundantly in the southeastern part of Cape Province, and important economically as a lumber tree. Its foliage differs from *P. Henkelii* in the shorter and smaller rigid leaves on erect twigs and fleshy receptacle, and from *P. elongatus* by the wider leaves with three vascular resin canals and no stomata on the upper side.

Podocarpus latifolius shows wide variation in its foliage as would be expected in a species of such wide distribution. It seems to be midway between *P. elongatus* and *P. milanjanus*, with many sterile specimens diffi-

† This symbol preceding the abbreviated name of an herbarium following the specimens examined signifies that the details of the leaves of this specimen have been examined in cross-section.

cult to classify because of extreme characters. The difference between juvenile and adult foliage, which has already been noted in a number of species, adds to the range of characters involved. A detailed description may be found in Chalk (3) and Stapf (10).

Of the varieties of this species which have been described, Stapf (10) and Chalk (3) disposed of most. However, the variety *P. latifolius* var. *latifolia* still standing deserves comment. With its long narrow leaves it seems that this should be a variety of *P. elongatus*, while the erect leaves around rigid twigs show a relation to *P. latifolius*. However, the leaves "1–2 in. long \times 2–3 lin. wide" are long narrow leaves and certainly belie Chalk's and Stapf's suggestion that it is the common form in the Cape Colony with its "short, wide leaves." Robyns (8) says that the green color of the receptacle, which has been given by certain authors as a distinctive character for *P. latifolius*, should not receive consideration. Stapf (10) indicates that, in a mature state, this receptacle is vividly colored red as in *P. milanjanus* and he describes it as resembling a "small dark red cherry in color and shape." It is hard to understand why Chalk (3), after using and quoting Stapf, used a green receptacle for a key character only a year later.

DISTRIBUTION: Limited at present to South Africa, most abundant in the southeastern part, probably ranging farther north but no collections seen.

SPECIMENS EXAMINED:

SOUTH AFRICA: Transvaal: Zoutpansberg, *Hutchinson & Gillett* 4283 (K—2 sheets), *Houseman* 5249 (K), *Obermeyer* 1228 (†F); Pietersburg, Houtboschberg, *Burt-Davy* 1194 (K); The Downs, Sabie, *Rogers* 21910 (K); Helpmakaar Arboretum, *Burt-Davy* 20252 (†A, †BR), *Leeman* 105 (†K); Blaauwburg, *Smuts* 906 (K); Waterberg, *I. B. Pole Evans* in 1933 (K); Nylstroom, *Burt-Davy* 4549 (†K), *Galpin* 11663 (†K). Swaziland: Forbes Reef Bush, *Burt-Davy* 2748; Kaaphe Kloof, *Rogers* 21089 (K), *Burt-Davy* 2455 (K). Orange Free State: Drakensburg, *Cooper* 1111 (†BM, K, NY). Natal: Zululand, Ngoya Forest, For. Dept. 4266, *Chilvers* (†A), *Wilson* in 1922 (A—2 sheets); Nat'l Park, Drakensburg, *Godman* 263 (†BM), *Hutchinson* 4488 (K); Champaign Castle, *Meebold* 13140 (NY); Durban, near garden, *Wilson* in 1922 (A), *Hout* in 1859 (K); Donneybrook, *Wilson* in 1922 (A); The Boyle, *Bews* in 1922 (A), *Wilson* in 1922 (A—2 sheets); Van Reenery Prop., *Kuntze* 1800 (K), *Gerard* 127 (K), *Sanderson s.n.* (†K). Cape Province: East Griqualand: Umzimkulu, Mhlunga Forest, For. Dept. Herb. Pret. 2168, 2170, 2189 (♀ & ♂) *Kaufmann* (K); Maclear Dist., Pot River Berg, *Galpin* 6831 (K); Emkazene Forest, Ingwangwane, For. Dept. Herb. Pret. 1957, *Houshold* (K); Instubani Forest, For. Dept. Herb. Pret. 2227, *Frazer* (K); Buswayo Forest, Manina, For. Dept. Herb. Pret. 2266, *Merwe* (K). Albany Division: near Grahamstown, *MacOwan* 1408 (F, K, YU), *MacOwan* 1958 in part (†GH, †K), *Wilson* in 1922 (A—2 sheets); w. of Grahamstown, *Zeyher* 3885 (K); Atherston, *Anon.* 89 (†K). Uitenhage Division: *Zeyher* 3880 (K). Knysna Dist.: Katzees Kraal, *Burchell* 5223, 5254 (†GH, K); Deepwalls Crown Forest, *Wilson* in 1922 (†A—2 sheets); Harberville Forest, *Keet* 524 (†K), *Bowie s.n.* (†K), *Burchell* 5223 (†K), *Wilson* in 1922 (A—2 sheets), *Munde & Maire* 1840 (K). George & Knysna: *Bowie s.n.* (K). George Dist.: *Drege* 1639 (K),

Burchell 5843 (†GH, K), *Burchell* 3505, 5843 (K). Cape Dist.: Table Mtn., near Brown's Krall, *Prior* in 1847 (K), *Wilson* in 1922 (†A—6 sheets), *Geehout* 12 (A), 223 (A), *Zeyher* 3533 (A); Stellenbosch, *Harvey s.n.* (†BM); Murchison, *Wood* 3028 (K); Newland woods, *Wolley Dod* 2729 (K); Groot Vader's Bosch, *Anon.* in 1906 (A), *Thunberg s.n.* (†UPS); Orange Kloof, *Gamble* 22002 (K); Oliphant's River, *Pillans* 5297 (†K); *Zeyher* 3882 (†K), 3883 (†K), *Munde & Maire s.n.* (†K). Cape Colony but no locality: *Anon.* in 1879 (CAS), *Drege s.n.* (†Mo), *Ecklon & Zeyher s.n.* (†A), *Burt-Davy* 4549 (†K), Corney Westliche, *Prager* 90 (†CAS), *Anon. s.n.* (K). No locality indicated: *H.R.P. ex Herb. A.C. Limingani Comit. A* (DS), *Anon. s.n.* (K).

CULTIVATED: South Africa: Tokai, near Capetown, *G.A.W.* in 1912 (K), *Eames* in 1939 (CU); Cleremont Garden, The Hill, *Wilson* in 1922 (A—5 sheets); Mission de Bunia, *Gilbert* 505 bis (†BR); Newlands, Kirstenbosch, *Compton* in 1941 (†Ill). England: Kew, *Cook* in 1937 (†Ill), *Buchholz* in 1950 (†Ill).

Podocarpus latifolius* var. *latior Pilger in *Pflanzenreich* IV. 5 (Heft 18): 90. 1903; Stapf in *Fl. Cap.* 5 (Sect. 2, suppl.): 7. 1933; Chalk et al., *For. Trees & Timbers Brit. Emp.* 3: 82. 1935.

A variety with very wide leaves, which is easily recognizable.

DISTRIBUTION: Cape Province on mountain slopes, apparently quite rare.

SPECIMENS EXAMINED:

SOUTH AFRICA: Cape Province: Vogelgat, *Schlechter* 9542 (K, †Ph); Table Mt., *Wilson* in 1922 (†A), *Drege*, in part, ex *Bernhardi Herb.* (†Mo).

Podocarpus Henkelii Stapf ex Dallimore & Jackson, *Handb. Conif.* 47. 1923, 1931, 71. 1948; Florin in *Svenska Vet.-Akad. Handl. ser. 3*, 10: 279. 1931; Chalk et al., *For. Trees & Timbers Brit. Emp.* 1: 23. 1932, 3: 84. 1935; Stapf in *Fl. Cap.* 5 (Sect. 2, suppl.): 9. 1933.

This tree is closely associated with *P. latifolius*, but can readily be distinguished by the larger, drooping, attenuate and often falcate leaves. Its description, distribution and regeneration is treated at length by Chalk et al (3). In certain areas it is found abundantly (Natal, East Griqualand) where it forms 90% of the trees in pure open forests. In leaf anatomy it shows a range of variation similar to that of *P. latifolius*, and juvenile specimens of *P. latifolius* are often difficult to distinguish from it.

DISTRIBUTION: South Africa, in Natal, Swaziland, northern Transvaal and East Griqualand.

SPECIMENS EXAMINED:

SOUTH AFRICA: Transvaal: *Barborton* 2467 (†K). Natal: Swaziland, Forbes Reef, *Burt-Davy* 2748a (†K), Pretoria For. Dept. 1880, *Houshold* (K); Swartzkop, *Sim* in 1921 (A—3 sheets); *Donnybrook*, *Wilson* on Feb. 16, 1922 (A—7 sheets); Kirstenbosch, *Sim* 1252/14 (†Ill); Pietermaritzburg, *Lindeberg* in 1936 (†A), *Wilson* on Feb. 12, 1922 (A), *Wilson* on Feb. 14, 1922 (A—3 sheets ♂, 3 sheets ♀). Griqualand East: Mt. Ayliff, Ft. Donald,

Balembu Forest, *Cochrane* in 1920 (†K—2 sheets); Nguhi Forest, *Cochrane* in 1920 (K); Gsewaleni Forest, Pret. For. Herb. 2172, *Cochrane* (K); Insikini riverside, *Dawson 1441* (†K). Cape Province: Knysna, *W. A. & C. B. Setchell* in 1927 (†UC). Locality unknown: *Ad No. 1282*, Ser. I, ex Herb. L. van den Bossche (†BR).

CULTIVATED: Africa: Tokai near Capetown, *Wilmot* in 1912 (K). England: Kew, Buchholz in 1950 (†III). United States: New York Bot. Garden in 1926 (†NJU).

Podocarpus milanjanus Rendle in Trans. Linn. Soc. ser. 2, 4: 61. 1844; Pilger in Pflanzenreich IV. 5 (Heft 18): 92. 1903, in Nat. Pflanzenfam. ed. 2, 13: 247. 1926; Dallimore & Jackson, Handb. Conif. 50. 1923, 1931, 75, 1948; Battiscombe, Desc. Cat. of Common Trees and Woody Plants of Kenya Colony 1. 1926; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 279. 1931; Chalk, Burt-Davy & Desch, For. Trees & Timbers in Brit. Emp. 1: 24. 1932; Robyns in Inst. Roy. Col. Belge, Bull., 6: 226. 1935, in Fl. du Congo Belge du Ruanda-Urundi 1: 6. 1948; Chevalier in Rev. Bot. Appl. 19: 411. 1939.

Podocarpus milanjanus has a very wide tropical distribution from 15° s. lat to 10° n. lat. and across the entire width of the continent. It has wider leaves than *P. elongatus*, but no anatomical differences in the leaves from those of *P. latifolius* and *P. Henkelii*. However, the natural areas of these species are so far removed from each other that there is little chance of confusion. *Podocarpus milanjanus* shows considerable variation in the foliage due to its appearance in all horizons of mountain forest, even into subalpine regions where the reduction in size of both the foliage and the tree is considerable. In general appearance, the leaves seem to be more spreading than those of *P. latifolius*, but the form of the young specimens is very similar. The leaf anatomy shows no consistent difference of specific importance other than that the rows of stomata seem closer together.

In comparisons made by Laurent (4), *P. milanjanus* exceeds *P. latifolius* and *P. elongatus* in the greatest dimensions of leaves, male cones, peduncles, and length of seed. Chalk et al. (2) include it in their key to African *Podocarpus*, distinguishing it from *P. elongatus* by the larger leaves, but from *P. latifolius* only by the red receptacle which has been mentioned before as an error.

In a recent study of specimens accumulated at the Brussels Herbarium, Robyns (8) found such extreme variation that at first he thought he had more than one species, but his detailed discussion gives adequate evidence that this is within the range of normal variation of the species. Moreover, there is extreme difference between adult and juvenile foliage. Hence, Robyns abandons Pilger's *forma arborescens* and *forma typica*, and substitutes the more descriptive *forme adulte*, *forme éricoïde*, and *forme juvénile*. He illustrates these by photographs of both foliage and mature tree habit in the case of *forme éricoïde*.

DISTRIBUTION: Africa, from Cameroons and southern Sudan, south through Belgian Congo, Uganda, Kenya, Tanganyika, into Nyasaland and

southern Rhodesia, on mountain slopes and alpine zones from 1900–3500 m. altitude.

SPECIMENS EXAMINED:

SUDAN: Immatong Mts., Ras Logoforsk, *Chipp* 104 (†K); Mt. Kivetti, *Chipp* 85 (K); Lomwaga Mt., E. Acholi, *Greenway & Hummel* 7281 (K), *T. Smith s.n.* (K—2 sheets). UGANDA: Immatong Mts., *Eggeling* 3600, 3564 (K); Kigezi, *Eggeling* 3245, 3247, 3249, 3251 (K); Mt. Elgon, *Snowden* 438 (A, K); Bulanbuli, *Snowden* 912 (†A—3 sheets, BR, K—2 sheets); Butandiga, *Snowden* 964 (A, K); Benet, *Eggeling* 2465 (BR, K), *Eggeling* 2470 (K); *Dummer* 3623 (K), *Lugard* 694 (K); Entebbe, *Dawe* 273 (K); S. Budde, *Dawe* 969 (K); Benet Sabei Bugishu, *Thomas* 2633 (K). BELGIAN CONGO: Ruwenzori: Nyam-bitaba, *Humphreys* 1402 (†BM); s. of Butahu River, Bambune, *Chapin* 83 (†NY); westside, *Chapin* 113 (BR, †NY), *Bequaert* 3703 (BR), *Humbert* 8903 (BR); Lukubuku valley, *Eggeling* 1259 (K); *Fishlock & Hancock* 160 (†K), *Dawe* 547 (K), *Scott-Elliott s.n.* (K), *Doggett s.n.* (K), *Lebrun* 4570 (BR, K), *Purseglove* 347 (K), *Esmans* 15 (BR); Tshiaberimu massif, between Kasindi & Lubango, *Lebrun* 4762 (†BR, K); Mt. Tsiaberimu, *Prince Leopold* 49, 50, 51 (†BR); Kahuzi Massif, *Humbert* 7716, 7716bis, 7716ter (†BR), *Scaetta* 1408 (†BR, K); Mt. Kahuzi, *Scaetta* in 1928 (†BR), *Lebrun* 5528 (K); Virunga Mts., Mushubangabo Volc. *Burt* 3158 (K); s. slope, Chambra-gongo Saddle, *Burt* 3169 (BR, K); Nyirangongo Volc., *Humbert* 7951 (BR); Nyamlagira Volc., *Humbert* 8148 (BR), *Heutmann* in 1938 (BR). Ruanda: Nyamusha-Kogunge, *Scaetta* 1722 (†BR); Rutengeria, *Lestrade* 1 (†BR). KENYA: Mt. Aberdare, *R. E. & C. E. Fries* 798 (BR, K); Mt. Kenya, west slopes, *Mearns* 1297 (†F, GH, NY—2 sheets, †US); Lari, *Wilson* in 1921 (A, †UC-seedling), (†A), (A—4 sheets); Nairobi, Kisumu, *Dummer* 1565 (K); Kikuga Hills, *Comm. at Morubasa* (K); Muzherengira, *Elliott* 251, 255 (K); *Whyte* in 1898 (K—2 sheets); *Hutchins* in 1907 (K—3 sheets); *Hutchins s.n.* (K); *Cooper* 843 (BR); *Imp. For. Inst.* 15a (A). TANGANYIKA: Mt. Kiliman-jaro, Bismarck Hill, *Greenway* 3879 (BR, K); s. slope between Umbwe & Weru-weru rivers, *Greenway* 3180 (K); *Schlieben* 4862 (BR); Pare Mts. Mushange, Kipare, *Greenway* 6544 (K); East Usambara Mts., *Greenway* 4673 (K), 4899 (K); Uluguru Mts., Lupanga Peak, Morogoro, *Burt* 4714 (A, K), *Schlieben* 3153 (BR, K); Kirunga Volc., *Kassner* 3202 (K); Kondo, Iringa Dist., *Burt* 1068 (K); Kinguassi Mt., *Burt* 920 (K), 971 (K), 1174 (K), 1345 (K—2 sheets), *Imp. For. Inst.* 70, *Wigg* (A), Mbalamu, *Adamson* 71, 72 (K). NYASALAND: north of Lake Nyasa, Kyimbila Dist., *Stolz* 387 (K); Rungwe Sta., *Stolz* 363 (GH, K); Mt. Malosa, *Whyte* in 1896 (†K); Mwanemba Point, *McClownie* 171 (K), *Johnston* in 1896 (†K), *Topham* 914 (K); below and w. of Lake Chiuta, *Cunningham* 10 (K); Mt. M'lanji, *Burt-Davy* 22023 (†A, †F), 22007 (BR), 22145 (BR), *Stolz* 373 (GH), *Whyte* 34, 39 TYPE (†BM), *Whyte* in 1891 (†K), *Buchanan* 949 (K—2 sheets), 969 (†K), *Clements* in 1924 (A), *Greenway* 3001 (K), *Greenway* 4673 (†K), *Greenway* 6300 (K). S. RHODESIA: Gazaland, Chimanimani Mts., *Swynnerton* 1962 (K); Umkali, Uumba, *Galpin* 9242 (K), *Dept. Agr.* 1167 (K); Mukungwa Valley, *Greenway & Trapnell* 5550 (K). ANGOLA: Nkanda Hills (Congo), *Dawe* 110 (†K); Dist. Bie, Cuito Rapids, N. Lisboa, *Gossweiler* 10975 (K); Sierra da Chella, Humpata, *Humbert* 16628 (†BM).

CULTIVATED: Tanganyika, *Comm. For.* A65/33 (A, BM, BR, †F, Ill, K, NY,

†Y); Horti Thenensis, *Luja* 77, *Ser. III* (†BR); Nursery Kinohop, Aberdeen Mt., *Wilson* in 1921 (A-seedlings); N. Rhodesia, Bot. Garden, *Burtt-Davy* 21883 (BR).

Podocarpus ulugurensis Pilger in Notizbl. Bot. Gart. Mus. Berlin 12: 82. 1934.

This tree, recently described from a single collection, resembles *P. milanjanus* except for several rather striking differences. The leaves of *P. ulugurensis*, contrary to the foregoing species, have a distinctly grooved upper midrib. According to the description, the male cones have thickly coriaceous scales 4 mm. long and the cone on the type specimen measures 3 cm. long and 4 mm. wide. Study of the leaf anatomy shows extreme thickening of the cell walls in all regions. Most surprising of all, two additional resin canals are seen in the transfusion tissue, a feature found elsewhere only in certain specimens of *Eupodocarpus* from the South Pacific, *P. longifoliolatus* in New Caledonia and *P. decipiens* in the Fiji Islands.

DISTRIBUTION: In the Uluguru Mts. of Tanganyika, 2200 m. elevation, in fog forests.

SPECIMEN EXAMINED:

TANGANYIKA: Uluguru Mts., *Schlieben* 4224 TYPE (†BR).

Podocarpus madagascariensis Baker in Jour. Linn. Soc. 21: 447. 1885; Pilger in Pflanzenreich IV. 5 (Heft 18): 92. 1903, in Nat. Pflanzenfam. ed 2, 13: 247. 1926; Laurent in Ann. Fac. Sci. Marseille 23: 53. 1915; Dallimore & Jackson, Handb. Conif. 50, 1923, 1932; 74. 1948; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 279. 1931.

Podocarpus madagascariensis, as indicated by Baker, is closely related to the foregoing species. It is a small tree indigenous to the island of Madagascar. Numerous specimens were collected by Perrier de la Bathie in 1912. An excellent study of the species and comparison with *P. elongatus*, *P. latifolius*, and *P. milanjanus* were made by Laurent (4). The size of foliage leaves and peduncle exceeds that of all the other species, and the seed (20 mm. long) is twice as large as that found in the other three species. The length of the male cone, 13 mm., is the least of any species in this group. Pilger's (6) suggestion that this species belongs to section *Stachycarpus* is unfounded.

The leaf anatomy shows the greatest degree of thickening of cell walls, to the extent that most of the mesophyll, including much of the palisade parenchyma, is thickened, with pitted walls, and much of it is devoid of cell contents. The large seed is blackish and oval in shape, 20 mm. long and 8 mm. in diameter.

DISTRIBUTION: On mountain slopes on the island of Madagascar.

SPECIMENS EXAMINED:

MADAGASCAR: Massif de Beampingaratra (Sub-Est), Mt. Papanga, *Humbert* 6398 (†A), *Baron* 2794, 3129, 3441 (†K); *Chouvenot* 107 (BM, †K); Kiknife Hills, *Warburg* 549 (K).

Podocarpus madagascariensis var. **rotundus** Laurent in Ann. Fac. Sci. Marseille 23: 59. 1915.

This variety grows at an altitude higher than that of the species. It possesses somewhat smaller leaves but larger seeds (28 mm. long).

DISTRIBUTION: Madagascar, on basalt at 1500–1800 m. altitude.

SPECIMEN EXAMINED:

MADAGASCAR: *Parker s.n.* (†Kew).

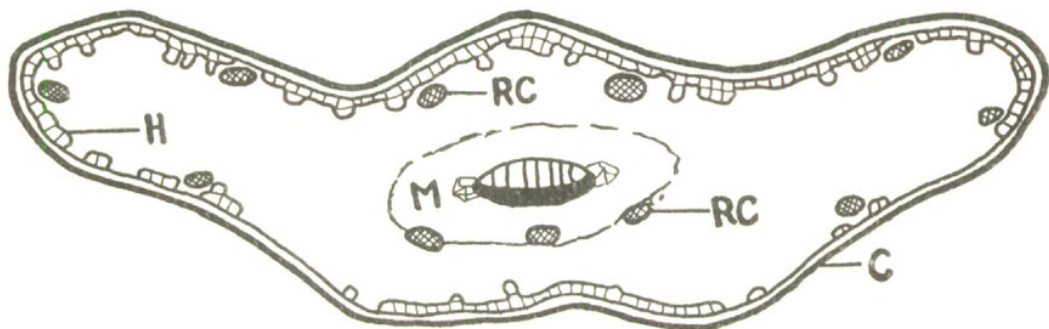
Podocarpus rostratus Laurent in Ann. Fac. Sci. Marseille 23: 60. 1915; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 262. 1931; Orr in Trans. Bot. Soc. Edinburgh 34: 11. 1944.

This extremely rare, and perhaps now extinct, species from the island of Madagascar, is different from all other podocarp species. It is a small tree, 8–10 m. high, with somewhat shiny leaves, 2.3–3.6 cm. long and 1.25–2 mm. wide, sessile, straight, very narrowly lanceolate, gradually attenuate toward apex. Male cones solitary and sessile or in groups of 2 or 3 on a slender, 5–6.5 mm. peduncle, 10–20 mm. long and 3 mm. wide, with scales triangular and apiculate. Female cones and seeds are unknown.

The leaf anatomy shows a single midvein with two very small lateral groups of transfusion tissue, all of which is surrounded by a thick layer of parenchyma definitely distinguishable from the rest of the mesophyll of the leaf by the dense cell contents. Below the vascular bundle are 3 resin canals, one central and two lateral. Laurent (4) found a thin sheet of "irrigation tissue" on each side of the vein separating the palisade from the spongy parenchyma. We do not find this to be lignified and pitted as in true accessory transfusion tissue. There is a continuous hypoderm on the upper side of the leaf, often more than one layer thick, and it is present also between the rows of stomata below. Differing from all other podocarps, it has a number of resin canals, 6–10, around the edge of the leaf just inside the hypoderm (TEXT-FIG. 1). These were described rightly by Laurent (4) as varying in number from one leaf to another and even within the same leaf according to the position near the base, middle, or apex. Also the arrangement of the stomata into two bands on each side of the midrib, on the lower side of the leaf, is a distinctive character. The stomata show a definite Florin ring. The lack of the female structures prevents exact placing of this species taxonomically.

Laurent (4) tried to place this species among its relatives. He compared it with *P. gracillimus*, *Nelson* 423 (which has been clearly shown to belong in section *Afrocarpus*), its foliage being the same shape, but *P. rostratus* differs from it, as expected. Because *P. gracillimus* was originally in the

section *Stachycarpus*, as expressed by Pilger (6), Orr (5) attempted to place it as an aberrant member of that section. The differences listed by him, and which we have confirmed, indicate clearly the section *Eupodo-*



TEXT-FIGURE 1. *Podocarpus rostratus* Laurent. Cross-section of leaf showing relative thickness of (C) cuticle, extent of (H) hypodermal fibers, location of marginal and vascular (RC) resin canals, and the special layer of (M) mesophyll surrounding the vascular bundle and transfusion tissue. $\times 50$

carpus where continuous upper hypoderm and the three vascular resin canals are compatible. In comparison with other species, we find *P. rostratus* most closely resembles *P. acutifolius* (New Zealand) in subsection D, which is found also in Chile and Australia. In all except two characters of the leaf anatomy *P. rostratus* matches *P. acutifolius*, even to the presence of the Florin ring in the stomatal subsidiary cells.

We are placing this species in a new subsection E of *Eupodocarpus* in recognition of the following anatomical features: (1) the presence of a variable number of marginal resin canals, different from the condition in all other podocarps; (2) the double stomatal bands on the lower side of the leaf, likewise not found in any other podocarps; (3) the three vascular resin canals found in African and Asiatic *Eupodocarpus* but not in sections *Afrocarpus* nor *Stachycarpus*.

DISTRIBUTION: Madagascar, on high summits of Mt. Tsaratana, in forests almost destroyed by fire.

SPECIMEN EXAMINED:

MADAGASCAR: Mt. Tsaratana, *H. Perrier de la Bathie* 10443 (†ex Florin, Riksmuseet, Stockholm).

LITERATURE CITED

1. BUCHHOLZ, JOHN T. & NETTA E. GRAY. A Taxonomic Revision of *Podocarpus*. I. The sections of the genus and their subdivisions with special reference to leaf anatomy. Jour. Arnold Arb. 29: 49-63. 1948.
2. CHALK, L., J. BURTT-DAVY & H. E. DESCH. For. Trees & Timbers Brit. Emp. 1: 20-26. 1932.
3. CHALK, L., M. M. CHATTAWAY, J. BURTT-DAVY, F. S. LAUGHTON, & M. H. SCOTT. For. Trees & Timbers Brit. Emp. 3: 69-90. 1935.
4. LAURENT, M. L. Les *Podocarpus* de Madagascar. Ann. Fac. Sci. Marseille 23: 52-64. 1915.
5. ORR, M. Y. The leaf anatomy of *Podocarpus*. Trans. Proc. Bot. Edinburgh 34: 1-54. 1944.
6. PILGER, R. Taxaceae. Pflanzenreich IV. 5 (Heft 18): 1-124. 1903.
7. PILGER, R. Taxaceae. Notizbl. Bot. Gart. Mus. Berlin 12: 82. 1934.
8. ROBYNS, W. Sur les especes de *Podocarpus* du Congo Belge et du Ruanda-Urundi. Inst. Roy. Col. Belge, Bull. 6: 226-242. 1935.
9. RICHARD, L. C. AND A. Comm. Bot. Conif. 1826.
10. STAPF, O. Podocarpaceae. Fl. Cap., ed. Hill, 5 (Sect. 2, suppl.): 3-14. 1933.

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Gray, Netta E. 1953. "A taxonomic revision of Podocarpus, VIII. The African species of section Eupodocarpus, subsections A and E." *Journal of the Arnold Arboretum* 34(2), 163–175. <https://doi.org/10.5962/bhl.part.27150>.

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